612.843.15:612.843.52

THE RELATION BETWEEN THE ROD AND CONE MECHANISMS IN THE AFTER-EFFECT OF SEEN MOVEMENT.

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I. Introductory.

It has often been argued that the rod mechanism of the retina represents a more primitive level of development than the cone mechanism. Parsons(1), for instance, considers that the relation between the cone mechanism and the rod mechanism resembles that between the epicritic and protopathic systems of cutaneous sensitivity postulated by Head. On that view the activity of the cone mechanism might inhibit the rod mechanism, as the epicritic system is supposed to inhibit the protopathic system. Experimental evidence of an inhibitory relationship between the rods and cones has been brought forward by Müller(2) in regard to certain phenomena of colour vision, by Creed and Granit(3) in the case of negative after-images, and by Granit(4) in the case of the after-effect of seen movement. On the other hand the results of the experiments of Porter(5) and Ives(6) on flicker, and those of König(7) on the variation of acuity with intensity of illumination, are difficult to explain on the assumption of inhibition; and, in fact, the form of the curves obtained by them suggests that in these cases the rod and cone mechanisms reinforce each other.

The evidence given by Granit in favour of inhibition between the rod and cone mechanisms in the after-effect of seen movement depends on measurements of the duration of the after-effect when a black and white moving object is viewed from various distances at various intensities of the illumination. Granit found that under certain conditions in which both rods and cones tend to be excited the duration of the after-effect is much smaller than would be expected. He attributes this to inhibition of one mechanism by the other. But it may be objected to the results obtained by Granit, that the effects attributed by him to inhibition might be ascribed at least in part to a qualitative change in the perceptual configuration resulting from the variation in distance of the object from the observer. The present paper describes experiments which were carried out to test Granit's conclusion by a different method.

II. Principle of the method.

It is known that red light of wave length greater than about 6700 Å.U. stimulates only the cones of the retina, and that blue or violet light stimulates the rods relatively strongly and the cones relatively weakly, while light of intermediate wave lengths stimulates both mechanisms to various extents. We should therefore expect on Granit's theory that the duration of the after-effect would depend on the colour as well as on the intensity of the light used to illuminate the moving object. The following method has therefore been adopted:

The after-effect is measured for two different areas of the retina; the light from the moving object stimulating firstly only the rod-free area, and secondly stimulating a larger area. In each case the after-effect is measured for red light of wave length greater than 6700 Å.U. and also for light of at least one other colour, the intensities of the light being approximately equal. Then it is clear that on Granit's theory the ratio of the duration of the after-effect with the larger area to the duration with the smaller area should be greater for the red light than for light of other colours, since when the larger area is stimulated by light of other colours there is mutual inhibition of the rods and cones. That is, if we call the durations of the after-effect for the red light and the large and small retinal areas LR and SR respectively, and those for the light of the other colour LC and SC respectively; then on Granit's theory the ratio $\frac{LR}{SR}\Big/\frac{LC}{SC}$ should be greater than unity.

III. Preliminary experiments with white light.

In some preliminary experiments the apparatus was rather similar to that used by Granit. The observer viewed a rotating drum 6 inches in diameter, marked with black and white stripes half-an-inch wide, from a distance of 7 feet. The retinal area stimulated could be varied by changing the size of a window in front of the drum. The drum was illuminated by a projection lantern in such a way that the illumination of the part visible through the window was approximately uniform, and the intensity of illumination was varied by means of diaphragms of varying aperture. The rest of the room was kept in darkness. In each experiment the drum was rotated for 30 seconds, while the observer fixated a small point of light in the middle of the visible part of the drum. The drum was then stopped, and the observer recorded the length of time for which it appeared to move backwards.

Measurements were made for two sizes of window (corresponding to visual angles of about 2° and about 5°) and for various intensities of illumination. The results were in general agreement with those of Granit, but it was found that there were very great individual differences between the results obtained by different observers, and between the results obtained by the same observer on different occasions. These differences were considerably greater than those to be expected from the curves published by Granit. For instance, in twenty observations under identical conditions the mean durations of the after-effect for six observers were 8·1, 6·9, 4·8, 0·8, 0·0, and 0·0 seconds respectively. (The last two observers could see no after-effect at all under these conditions.) These individual differences have not been explained.

An attempt was made to measure the after-effect with monochromatic illumination, light filters being placed in the plate-holder of the lantern, but with the available source of light it was not found possible to obtain sufficiently intense monochromatic illumination of the drum by this method.

IV. Experiments with monochromatic illumination.

In a second series of experiments the moving object was in the form of a grating through which monochromatic light was transmitted, and it was viewed through a system of lenses. This arrangement made it possible to use much brighter monochromatic illuminations than in the previous experiments.

Fig. 1 is a diagram of the apparatus. The moving object consisted of a trolley *TT* on which was mounted a system of vertical strings *SS*. These strings were wound over hair combs on a wooden frame. The trolley could be made to move at a slow and uniform speed in the direction of the arrow. Behind the trolley was a box containing a powerful electric lamp L_1, the bulb being of white glass. Light filters could be placed at *FF*. In front of the trolley was a square glass window *WW*, the size of which could be varied, and in the middle of the window was a black spot of 1 mm. diameter which served as a fixation point.

The observer viewed this system through an eyepiece *E* and an object glass *O*. A mirror *M*, from the middle of which a rectangular area of silvering had been removed, a lamp L_2 and filters and dimming slides at *F′F′* made it possible to vary the colour and brightness of an area of the visual field surrounding the moving object. In all the experiments this surrounding area was of the same colour and intensity as the light

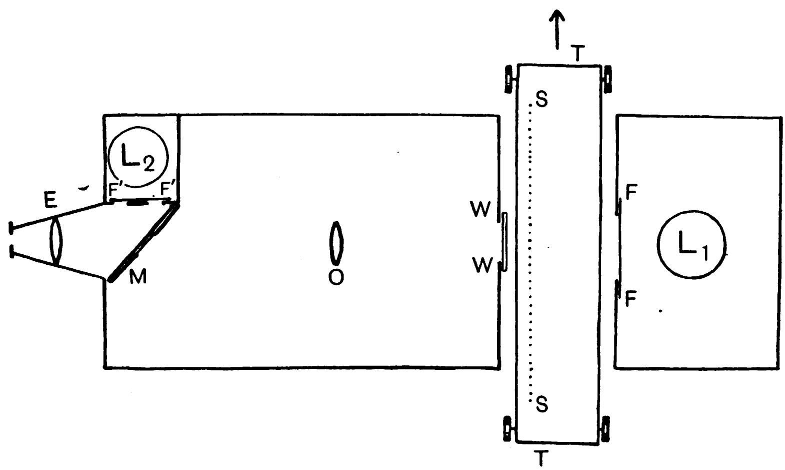

Fig. 1.

Fig. 2.

transmitted through the moving object. The field of view of the observer was therefore as is shown in Fig. 2; the moving lines in the centre of the field being surrounded by a black margin, outside which was a surrounding area of the same colour and intensity as the bright lines. (It was found that the presence of this illuminated surrounding area made the duration of the after-effect much longer and easier to measure.)

Three different wave lengths of approximately monochromatic light were obtained by the use of appropriate Wratten light filters or combinations of filters—red light of above 6800 Å.U., green light from about 5100 Å.U. to about 5700 Å.U., and violet light from about 3500 Å.U. to about 4600 Å.U. In each observation the trolley was made to move for 40 seconds and then stopped. The observer then continued to fixate the black mark in the middle of the window, and recorded the length of time for which the lines appeared to move backwards. In each series of readings two observations were taken in succession with a given colour and size of window, and the conditions were then changed. The various colours and sizes of window were given in different orders in different series of readings.

V. Results with monochromatic illumination.

A number of experiments were made with windows corresponding to visual angles of 2° (small window) and 4·5° (large window). The intensity of the monochromatic lights was such that they were judged (by direct comparison) to be of the same brightness as a white surface illuminated with an intensity of 2 foot-candles. Table I shows the mean duration of the after-effect for four subjects under these conditions, each of the numbers given representing the mean of twenty observations.

Table I.

Duration of after-effect in seconds

	Red		Green		Violet	
Subject	Small window	Large window	Small window	Large window	Small window	Large window
F. C. B.	12·3	12·4	11·2	13·8	10·4	11·7
J. M. B.	5·7	8·9	7·4	11·6	10·2	10·4
M. E. M.	4·1	5·7	4·0	5·0	3·2	4·8
M. D. V.	5·9	9·1	8·5	8·8	4·4	7·3
Mean duration	7·0	9·0	7·7	9·8	7·0	8·5

The mean value of the ratio $\frac{LR}{SR}\Big/\frac{LC}{SC}$ for the red and green lights is 1·04, and that for the red and violet lights is 1·06. It is quite clear from the variations in Table I that the differences between these ratios and unity cannot be regarded as significant, so that the results under these conditions do not give any evidence of interaction between the rods and cones.

Another series of experiments was made under conditions calculated to increase the amount of rod activity. The large window was made larger so that it now corresponded to a visual angle of 8° (the small window still being 2°), and the intensity of the light was reduced to about 0·05 foot-candles. The subjects were given 1 minute for partial dark adaptation before each observation. Three subjects were employed and twenty observations were made by each subject with each size of window with red and violet lights. The mean values of the ratio $\frac{LR}{SR}\Big/\frac{LC}{SC}$ for the three subjects were 0·72, 0·90, and 0·96 respectively. The fact that these ratios are less than unity might be taken to indicate that the action of the rods reinforces that of the cones under these conditions; but, as in the previous experiments, the differences cannot be regarded as significant.

The subject's introspections did not show any significant qualitative differences in the nature of the after-effect with the lights of different colours. With all colours the after-effect was very variable in its nature. Sometimes it was rapid and sometimes very slow, and it varied from a steady movement coming to a sudden stop to a succession of jerks.

VI. Discussion.

It is difficult to calculate the value of the ratio $\frac{LR}{SR}\Big/\frac{LC}{SC}$ to be expected under these conditions if Granit's theory is true. Granit expresses the intensity of illumination in his experiments as a fraction of "daylight," and not in absolute units; and in several other respects the conditions of these experiments were not strictly comparable with his. But if his explanation be correct one would expect from the curves published by him that the value for the ratio $\frac{LR}{SR}\Big/\frac{LC}{SC}$ in my experiments would be very considerably greater than unity. In the second series of experiments (when the large window corresponded to a visual angle of 8°) one would expect the ratio to be at least 2. It seems, therefore, that Granit's results must be explained by some hypothesis other than that of inhibition between the rods and cones. Perhaps, as has already been suggested, the explanation is to be found partly in the changes in the perceptual configuration when the distance of the moving object from the observer is changed.

It is possible that under conditions in which there is a greater amount of rod activity it may be found that there is some kind of inter-action between the rods and cones in the production of the after-effect. It is even possible that both in Granit's experiments and in mine the amount of rod action may have been negligibly small. All that my experiments can claim to show is that at present no satisfactory evidence exists of inter-action between the rod and cone mechanism in the production of the after-effect. The evidence of inter-action between the two mechanisms in the production of other visual phenomena seems to indicate the occurrence of inhibition in some cases and of reinforcement in others, as has been pointed out in § I. Much further work will be required before any general statement can be made about the relationship between the two mechanisms.

VII. Summary.

Some experiments have been performed to test Granit's theory that in the production of the after-effect of seen movement the rod mechanism of the retina tends to inhibit the cone mechanism. No evidence of inhibition was found, and it is suggested that Granit's results must be explained in some other way.

I wish to thank Mr F. C. Bartlett, who suggested this research, for his help and advice.

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